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Intensified agricultural use of grasslands reduces growth and survival of precocial shorebird chicks

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Summary

1. Intensification of agricultural use of grassland habitats has been linked to the declines of many farmland bird species, several of whom have been in decline for multiple decades despite agri-environmental schemes. In the Netherlands, where most grasslands have been transformed into well-drained monocultures managed for maximal dairy production, schemes that aim to protect nests from agricultural activities are the most popular. The cause of the failure of these schemes, however, seems poor recruitment of farmland birds.

2. Using the black-tailed godwit *Limosa limosa limosa* as our model species, we tested the hypothesis underlying the most popular agri-environmental schemes that there are no differences in condition at hatch, growth, and apparent survival rates between chicks raised on monocultures compared with chicks from herb-rich meadows with high water tables, often managed, for the sake of grassland birds, in traditional ways. We also compare the growth rates from both habitat types with those of chicks from dairy farmland from 1976 to 1985, a time when population declines of godwits first became visible.

3. Hatchling mass did not differ between chicks from herb-rich meadows and grassland monocultures, but chicks hatched on monocultures were on average 14–16% lighter at fledging, and had 4% smaller bills than chicks hatched on herb-rich meadows. The growth rates of female chicks hatched on herb-rich meadows were similar to those of chicks measured from 1976 to 1985. Males fledged lighter and smaller than females.

4. Apparent survival during the first year of life for chicks hatched on herb-rich meadows was 2·5 times higher than that of chicks hatched on grassland monocultures. The apparent survival on herb-rich meadows seems sufficient for a stable population.

5. *Synthesis and applications:* We found striking differences between chicks hatched on modern grassland monocultures and herb-rich meadows. That chicks hatched on monocultures had lower growth and survival rates than chicks on meadows indicates that these chicks suffer a higher risk of starvation and/or predation. These findings imply that the most often applied agri-environmental schemes (i.e. payments per clutch found and postponed mowing), are not effective. Instead, these schemes could even encourage maladaptive habitat choice. Conservation efforts should thus focus on the provision of herb-rich meadows with high groundwater tables.

Key-words: agricultural intensification, black-tailed godwit, farmland, Gompertz curve, habitat management, *Limosa limosa*, mark–recapture, meadow birds, waders, wet grassland

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Introduction

The population declines of farmland birds over the last decades tend to be associated with insufficient recruitment linked to an intensification of agricultural land use (Chamberlain *et al.* 2000; Donald, Green & Heath 2001; Vickery *et al.* 2001; Newton 2004; Roodbergen, van der Werf & Hötker 2012). Intensification of grassland use, mainly for dairy farming, is characterized by lowering of groundwater tables, strongly increased use of fertilizers and regular re-seeding with fast-growing protein-rich grass species, leading to higher stocking densities in some areas and earlier and more frequent mowing in others (Newton 2004; Tscharntke *et al.* 2005; Kleijn *et al.* 2010; Groen *et al.* 2012). Currently, agricultural grasslands are being mowed during the nesting phase of many ground-nesting bird species, such as whinchat *Saxicola rubetra* (Grüebler *et al.* 2012), bobolink *Dolichonyx oryzivorus* (Bollinger, Bollinger & Gavin 1990), Eurasian skylark *Alauda arvensis* (Donald *et al.* 2002) and corn bunting *Emberiza calandra* (Perkins *et al.* 2011). Mowing leads to nest losses and losses of young chicks (Schekkerman, Teunissen & Oosterveld 2009; Tyler, Green & Casey 1998), but it also reduces cover and food availability (Britschgi, Spaar & Arlettaz 2006; Schekkerman & Beintema 2007; Kleijn *et al.* 2010) for precocial chicks foraging on insects.

To stop the decline of meadow bird populations, national and European conservation schemes have been in use now for several decades (Whittingham 2007; Kleijn *et al.* 2011). In the Netherlands, the most popular schemes are the ones in which farmers are compensated for loss of income incurred by later mowing, or by leaving a strip of uncut grass around nests to spare them during agricultural activities (Verhulst, Kleijn & Berendse 2007; Breeuwer *et al.* 2009), but which allow the highly intensive use of agricultural land to continue (Kleijn *et al.* 2011; Musters *et al.* 2001; Schekkerman, Teunissen & Oosterveld 2008). However, postponed mowing in otherwise intensively managed grassland monocultures often creates a sward so dense that chicks may find it difficult to move around (Devereux *et al.* 2004) and may incur reduced food intake rates (Kleijn *et al.* 2010).

In addition to these popular agri-environmental schemes (AES) for dairy farmers competing on the world market, specially managed areas for birds have been set-up. These areas are often owned by nature conservation organizations, and they are either managed by these organizations or by farmers who lease the meadows, or they are part of the highest-level AES with strict rules on how to farm. In these areas, agricultural land use resembles the use in an era when meadow-breeding bird populations were thriving (Groen *et al.* 2012): groundwater tables are kept high, less and more-fibre-rich types of manure are applied, and mowing and other activities on the land overlap as little as possible with incubation and chick rearing periods. Such grasslands have a more open vegetation structure and are much more diverse in terms of plant species and vegetation structure (Bakker & Berendse 1999; Groen *et al.* 2012), insects (Hendrickx *et al.* 2007) and birds (Donald, Green & Heath 2001) than the intensively managed grasslands.

However, despite this wealth of AES, the numbers of grassland birds continue to decline, whilst the underlying cause of insufficient recruitment of birds breeding in intensively used grassland monocultures has remained surprisingly understudied. Schekkerman & Beintema (2007) suggest that energy intake on grassland monocultures is insufficient for chicks of black-tailed godwits *Limosa limosa limosa*, a subspecies mainly breeding in the Netherlands, to grow at normal rates, whilst lower growth rates may lead to reduced survival. Here, we compare growth and survival of chicks growing up in grassland monocultures and in herb-rich wet meadows (often specially managed for meadow birds). We test the assumption underlying current popular agri-environment reward policies that chicks hatched on grassland monocultures have similar growth and survival as chicks hatched on herb-rich meadows. To put our measurements into a historical perspective, we provide a comparison with growth rates of chicks measured between 1975 and 1985 (Beintema & Visser 1989), a time when the godwit population had just begun its decline (van Dijk *et al.* 2010).

Materials and methods

STUDY AREA

The study was carried out in south-west Friesland, the Netherlands (52°55′N, 5°25′E), on 8480 ha agricultural land (Fig. 1). This area traditionally has held high densities of breeding black-tailed godwits (Mulder 1972; Beintema, Moedt & Ellinger 1995), but numbers have been in decline here as well (Weidevogelmeetnet Friesland unpubl. data). Fields were classified on the basis of herb richness and the occurrence of foot drains, as this accurately summarizes the intensity of modern agricultural management (Groen *et al.* 2012). Herb-rich meadows (80% of the study area) contained diverse grass and herb species and had groundwater tables not more than 30 cm below surface, while grassland monocultures (20% of the study area) had lower water tables, consisted dominantly of reseeded high-productive ryegrasses (*Lolium* sp.), and most were cut during the breeding period, usually with attempts to spare the nests marked by volunteers. To indicate the two types of agricultural habitat, we chose to use the terms 'meadows' and 'monocultures'. Arable fields (11% of the study area), usually for growing corn *Zea mays,* were also classified as monocultures. Between 2004 and 2006, we only studied godwits breeding on meadows, but from 2007, we extended the study area to also include monocultures. Black-tailed godwits are migratory, and present in the study area from early March until mid-July (Gill *et al.* 2008).

CHICK GROWTH AND CONDITION

Godwit chicks leave the nest within hours of hatching; we therefore used egg flotation (Liebezeit *et al.* 2007) to predict hatching

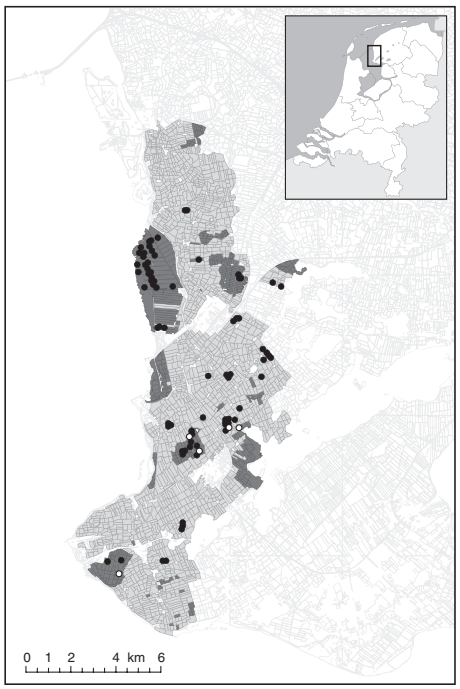

Fig. 1. Study area and nest locations of recaptured black-tailed godwit chicks. Black dots are chicks that remained on the same habitat type, the 5 white dots are chicks that moved from monocultures (light shading) to meadows (dark shading) or the other way around.

date so that we could ring and measure newly hatched chicks while still in the nest. Because of their crypsis, godwit chicks are difficult to find during the pre-fledging phase (*c*. 25 days), but we succeeded in recapturing 97 of 2155 chicks ringed in the nest. From 2004 to 2010, we recaptured, respectively 6, 13, 3, 8, 21, 7 and 2 chicks in meadows, and from 2007 to 2010 21, 8, 5 and 3, respectively, in monocultures. We measured body mass to the nearest 0·1 g using an electronic pocket scale, and bills to the nearest mm using callipers (although we miss data on bill length from 8 chicks). Chicks older than 5 days were weighed to the nearest 1 g on a larger scale.

The sex of the chicks was determined by genetic sexing, for which we obtained 30-μl blood samples, bleeding the leg vein of hatchlings and the brachial vein in older chicks. Blood was stored in individual 1·5-ml Eppendorf tubes containing 97% alcohol buffer and frozen at −80 °C as soon as possible (usually within days or weeks). The genetic sexing techniques used here are described in full by Schroeder *et al*. (2010).

We compared growth in body mass of the recaptured chicks with the Gompertz curve that Beintema & Visser (1989) derived for godwit chicks of known age caught between 1976 and 1985. The formula for the Gompertz curve is:

$$W = A * e^{-e^{-K(t-T)}}$$

where W is body mass, A is asymptotic body mass, K is the growth coefficient, T is the inflexion point and t is age in days (Winsor 1932). Beintema & Visser (1989) found the values $A = 273$, $K = 0{\cdot}085$, $T = 11$. We calculated a residual body mass for recaptured chicks in our study by subtracting their mass with the mass predicted by the Gompertz curve. We used birth location to indicate habitat type (herb-rich meadows or monocultures) on which they grew up. Although they can travel up to 3 km (Melter, Hönisch & Tüllinghoff 2009), only 5 chicks, all older than 14 days, were found on a different habitat type than where they hatched, and the furthest chick was found *c*. 1 km from its nest location. Smaller chicks are less capable of moving large distances than bigger chicks, thus in the first weeks during growth they are likely to remain in the habitat where they were hatched.

APPARENT SURVIVAL RATES

In the years 2004 until 2010, chicks were marked in the nest with a metal ring, and from 2008 to 2010 also with a plastic flag engraved with a unique code of three characters. The engraved leg flag enabled us to identify individuals with a telescope from a distance. These resightings in subsequent years were used to calculate and compare apparent survival probabilities of chicks hatched on meadows and monocultures. For this analysis, we used all resightings from 1 January of the year after their hatching until the end of the breeding season of 2011. However, chicks older than 10 days that were (re)captured were given a colour ring combination comprising one flag and four coloured rings, which are more easily seen from large distances. Younger chicks have legs too small for these colour ring combinations. Of 918 chicks marked between 2008 and 2010 in the nest with an engraved leg flag on meadows, 26 were recaptured at an age where we could replace the leg flag. On monocultures, we recaptured 14 of the 441 chicks marked in the nest, a similar proportion as on meadows. These older re-ringed chicks were not taken into account in the analyses of small chick survival because of the higher resighting probability; the number recaptured was too low to incorporate them with a different resighting probability in the mark–recapture analysis. A separate mark–recapture analysis for older chicks marked with a colour ring combination was carried out to estimate survival of chicks older than 10 days. From 2007 to 2010, we marked 132 chicks (average estimated age 15 days) with a colour ring combination on meadows, and 74 chicks (average estimated age 16 days) on monocultures, both including newly captured chicks and recaptures of chicks marked in the nest. With the estimates of the mark–recapture models, we calculated how many of the chicks marked in the nest whose engraved leg flag then changed into a colour ring combination would have survived. The unbiased chick survival rates are the number of chicks that would have survived the first year divided by the total number of chicks ringed in the nest.

The percentage of returned chicks and the number of study years were too low to include year-dependence in the estimates of survival and/or recapture rate. Consequently, both for chicks with leg flags and with colour ring combinations, we tested whether apparent survival from hatching until the second calendar year differed between chicks hatched on the two categories of agricultural land. Assuming that resighting probabilities of returning birds did not differ for individuals hatched in the two habitats, but given the variation in the age of first return to the breeding area (either in the second or third calendar year, Groen & Hemerik 2002), we tested two survival models: ϕ(a2-g/.)p(a2) and ϕ(a2-./.)p(a2). Here, ϕ is apparent survival, p resighting probability, g is habitat type (monoculture or meadow) and a2 stands for two age classes.

STATISTICS

We used R 2.13.0 (R Development Core Team 2011) for statistical analyses. With a linear mixed-effect model (nlme package), we compared mass and bill length on meadows and monocultures, after controlling for year, hatching date, their interaction and sex, with nest as random factor (Schroeder *et al*. 2008, 2012), of chicks newly hatched between 2007 and 2010. Mean hatching date (18 May) was subtracted from hatching date, so that intercepts are easier to interpret.

We then tested if growth differed for chicks hatched on meadows and monocultures using residual body mass derived from the Gompertz curve as response variable, and whether it differed from the chicks caught between 1976 and 1985. Older chicks can deviate more strongly from the Gompertz curve than younger chicks, leading to heteroscedasticity in the data. Therefore, we used linear models using generalized least-squares and the fixed weight variance function with the gls() function (nmle package). In addition to habitat type, we tested if there was an effect of hatch date, age (in days), sex and the interactions habitat type × hatch date, habitat type × age and age × sex. We tested effects of age × sex on residual body mass, because size dimorphism may appear during growth and may confound the results. Because sample sizes of 2009 (3 females, 4 males) and 2010 (4 females, 1 male) were low, we did not include a year effect.

From an age of *c*. 5 days until fledging, godwit bills grow linearly (Beintema & Visser 1989, and Fig. 4). This makes it possible to use linear statistical models. Because there was (almost) no difference in bill length for chicks just hatched in the two types of habitat (see Results), we selected chicks older than 5 days to compare bill growth of chicks hatched on meadows and monocultures. To test if bill lengths differ between the two types of grasslands, we used as main factors habitat type, hatch date, age, sex, and the interaction terms of habitat type × hatch date, habitat type × age and age × sex.

Models were fitted with the maximum likelihood fits for model comparison and subsequent simplifications. Effect sizes are given after restricted maximum-likelihood model fit. The effect of habitat type on bill growth was tested with the lm() function (stats package) for linear models.

Mark–recapture analysis was performed with the program MARK (White & Burnham 1999). Because the fullest model had an age structure and no time-dependence, we used the median $\hat{c}$ method integrated in the program MARK to test for goodness of fit. For the analysis with chicks marked with an engraved leg flag, we used the estimated $\hat{c}$ of 2·3 (± 0·03 SE), and for the older chicks with a colour ring combination $\hat{c}$ = 1·2 (± 0·01 SE), both based on 100 iterations, to correct for a slight overdispersion of the data. We used Akaike's information criterion corrected for small sample size (AICc) for model selection and inference (Burnham & Anderson 2002). Sample sizes used in the analyses are presented in Table 1.

Results

BODY SIZE OF NEWLY HATCHED CHICKS

The average mass of newly hatched chicks for all years was 28·4 g (SE ± 0·09). Hatchling mass did not differ between birds from nests on meadows and from monocultures (Table 2). Hatchling mass differed between years, but there was no effect of hatch date or sex. The average bill length at hatch for all years (17·2 mm, SE ± 0·04) did not differ between chicks hatched in the two types of farmland, although there seems to be a trend that chicks hatched on monocultures had slightly smaller bills (P = 0·05, bills differ with 0·15 mm, Table 2). Bill length differed between years, and males had 0·4 mm smaller bills at hatching (Table 2).

GROWTH IN RECAPTURED CHICKS

Of the 97 chicks that were recaptured, 37 were hatched on monocultures and 60 on meadows (Fig. 1). One chick moved from a monoculture to a meadow and was recaptured at 14 days at ± 650 m from its nest. The four chicks that moved from a meadow to a monoculture were all older than 16 days and were caught between 350 and 1000 m from their nest sites.

Figure 2 shows the growth in body mass of chicks caught on meadows and monocultures between 2004 and 2010 together with the Gompertz curve describing the growth of chicks caught from 1976 to 1985 (Beintema & Visser 1989). Female and male chicks hatched on monocultures from 2007 to 2010 were lighter the older they became when compared with the Gompertz curve, with male chicks showing greater deviations (Table 3 and Fig. 3). Females hatched on herb-rich meadows did not deviate significantly from the Gompertz curve the older they became, although males hatched on meadows did (again, they were lighter). The difference in mass between males and females increased with age, with males being 36 g lighter at fledging than females. At 184 g, females hatched on monocultures were 14% lighter at fledging (at 25 days) than females hatched in meadows (212 g). At 147 g, males hatched on monocultures were 16% lighter at fledging than males hatched on meadows (176 g). Hatch date and the interaction term habitat type × hatch date were not significant.

Recaptured female and male chicks that hatched on monocultures had smaller bills than chicks of the same sex hatched on meadows (Table 4, Fig. 4), although the interaction term of age × habitat type was not significant (P = 0·19), indicating that unlike body mass gains, the rate of bill growth did not differ significantly between grassland types. Because we found no difference in bill length of hatched chicks for both habitat types, this difference either appeared in the first 5 days, or the difference in rate of bill growth was too small to become statistically significant with our sample size. Male chicks ≥ 5 days old had bills that were on average 3 mm (± 0·8 SE) shorter than the bills of females, a difference that was maintained during the remainder of the prefledging period (Table 4). Females hatched on monocultures had at fledging a 4% shorter bill than females hatched on meadows (51 mm), and males hatched on monocultures a 4% shorter bill than males hatched on meadows (48 mm).

Table 1. Sample sizes of measured and marked godwit chicks used in statistical analyses. For the growth analyses, we used chicks of known sex measured in 2007–2010. For the bill length analysis, we used chicks older than 4 days. For the survival analyses, leg flags were only used in 2008–2010, but colour ring combinations in 2007–2010

	Freshly hatched		Recaptured*			Survival	
N	Mass	Bill	Mass	Bill	*N*	Leg flags	Colour ring combination
All	1205†	1211‡	77	69	All	1319	206
Males	614	615	36	27	Meadow	892	132
Females	591	596	21	20	Monoculture	427	74

*For statistical analysis we used data from 2007–2010.
†In 543 nests.
‡In 546 nests.

Table 2. Mixed linear model results on the mass and bill length of newly hatched black-tailed godwits. Estimates of non-significant terms are from the last model before simplification. The final model is shown in bold

Mass (in g)	Estimate	±SE	DF	*t*	*P*
Intercept	**28·34**	**0·20**	**662**	**139·11**	**< 0·001**
Habitat type*					
Monoculture	0·07	0·20	660	0·32	0·75
Hatch date	0·00	0·01	659	−0·07	0·95
Year†					
2008	**0·09**	**0·28**	**539**	**0·31**	**0·75**
2009	**0·47**	**0·28**	**539**	**1·66**	**0·10**
2010	**−0·29**	**0·26**	**539**	**−1·10**	**0·27**
Year × hatch date					
2008	0·06	0·04	656	1·64	0·10
2009	0·03	0·03	656	1·09	0·27
2010	0·05	0·03	656	1·94	0·05
Sex‡	−0·12	0·10	661	−1·13	0·26
Random effects					
σ_{nest}^2	**1·92**				
$\sigma_{residual}^2$	**1·46**				
Bill (in mm)					
Intercept	**17·03**	**0·08**	**663**	**205·37**	**< 0·001**
Habitat type*					
Monoculture	−0·15	0·08	662	−1·94	0·05
Hatch date	**−0·01**	**0·00**	**663**	**−2·33**	**0·02**
Year†					
2008	**0·23**	**0·11**	**542**	**2·15**	**0·03**
2009	**0·49**	**0·11**	**542**	**4·32**	**< 0·001**
2010	**0·61**	**0·10**	**542**	**6·17**	**< 0·001**
Year × hatch date					
2008	−0·02	0·01	659	−1·41	0·16
2009	−0·02	0·01	659	−2·14	0·03
2010	−0·02	0·01	659	−1·73	0·08
Sex‡	**−0·37**	**0·05**	**663**	**−7·63**	**< 0·001**
Random effects					
σ_{nest}^2	**0·64**				
$\sigma_{residual}^2$	**0·71**				

*Reference type is meadow.
†Reference year is 2007.
‡Reference sex is female.

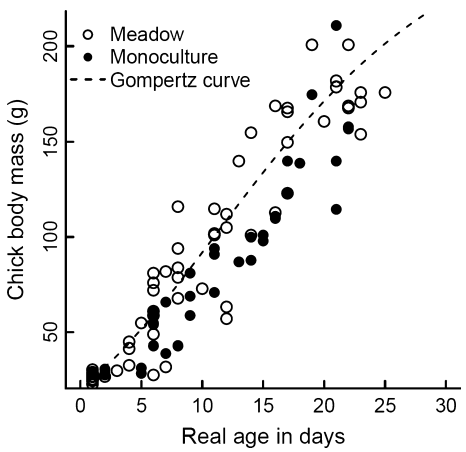

Fig. 2. Body mass growth of known-age black-tailed godwit chicks hatched on either meadows or monocultures in 2004–2010. The curve is not fitted to these data but represents the Gompertz curve of Beintema & Visser (1989) for chicks caught in 1976–1985.

APPARENT SURVIVAL RATES

The survival model for chicks with engraved leg flags ringed in the nest, which includes habitat type ϕ(a2-g/.)p(a2) was better supported than the model without habitat type ϕ(a2-./.)p(a2), delta QAICc = 4·4. The apparent survival estimate for chicks hatched on meadows was 0·13 (± 0·04 SE), and 0·04 (± 0·02 SE) for chicks hatched on monocultures. See Table 5 for all parameter estimates.

For the older chicks marked with a colour ring combination, the model with habitat type had with delta QAICc = 1·0 less support. Because this model did not lower the AICc while adding one parameter, this is not a competing model (Arnold 2010). Therefore parameter estimates were comparable (Table 5) and we used the model without habitat type for further calculations.

Using these apparent survival rates, we calculated that on meadows 116 of the 892 chicks marked with a leg flag survived, and 14 of the 26 recaptured as older chicks. Chicks hatched on meadows therefore had an apparent survival rate of 0·14. On monocultures, of the 427 chicks marked with a leg flag 17 survived and 8 of the 14 recap-

Table 3. Results of the generalized least-square model examining the effect of habitat type at hatch on the residuals with Gompertz curve of pre-fledged chicks of known sex. Estimates of excluded terms are from the last model before simplification. The final model is shown in bold

Deviation from Gompertz curve (mass in g)	Estimate (g)	±SE	*t*	*P*
Intercept	**−0·01**	**4·77**	**−0·00**	**1·00**
Habitat type* Monoculture	**2·28**	**3·94**	**0·58**	**0·58**
Hatch date	−0·14	0·20	−0·71	0·48
Age	**0·45**	**0·46**	**0·99**	**0·33**
Sex†	**0·12**	**5·32**	**0·02**	**0·98**
Habitat type* × hatch date	−0·20	0·43	−0·47	0·64
Habitat type* × age	**−1·24**	**0·50**	**−2·50**	**0·02**
Sex† × age	**−1·45**	**0·54**	**−2·72**	**< 0·01**

*Reference type is meadow.
†Reference sex is female.

Table 4. Results of the ANCOVA on bill length of black-tailed godwit chicks older than 5 days for pre-fledged chicks with known sex. Estimates of excluded terms are from the last model before simplification. The final model is shown in bold and has $R^2 = 0{\cdot}88$

Bill length	Estimate (mm)	±SE	*t*	*P*
Intercept	**20·92**	**1·40**	**14·99**	**< 0·001**
Habitat type* Monoculture	**−1·80**	**0·78**	**−2·30**	**0·03**
Hatch date	−0·03	0·05	−0·65	0·52
Age	**1·21**	**0·08**	**16·06**	**< 0·001**
Sex†	**−3·24**	**0·81**	**−4·00**	**< 0·001**
Habitat type* × hatch date	0·12	0·10	1·24	0·22
Habitat type* × age	0·00	0·16	0·00	1·00
Sex† × age	−0·12	0·16	−0·78	0·44

*Reference type is meadow.
†Reference sex is female.

tured older chicks. Chicks hatched on monocultures had an apparent survival rate of 0·06, a difference of 2·5 times.

Discussion

Over the last few decades, the majority of the wet, herb-rich meadows, the traditional breeding habitat of grassland bird species in the Netherlands, were transformed into intensively managed grassland monocultures (Kleijn *et al*. 2010; Groen *et al*. 2012). Here, we showed that godwit chicks hatched on such modern agricultural monocultures had a two-and-a-half-fold lower chance to make it to adulthood than chicks hatched on herb-rich meadows. The less pronounced difference in chick survival of older chicks on the two habitat types, despite a considerable difference in body mass at fledging, suggests that chicks younger than 10 days experience the highest mortality on monocultures. We must reject the hypothesis that there are no differences between the fates of chicks hatched and raised on herb-rich meadows and monocultures.

The lower apparent survival estimate of chicks hatched on grassland monocultures may be caused by: (i) low food availability (indicated by smaller growth rates), (ii) higher predation rate or (iii) a combination of both.

RELATIVE GROWTH RATES

Godwit chicks growing up on monocultures were smaller and lighter than chicks from meadows. The difference in growth rate suggests that prey quality and/or prey capture rates were lower on monocultures than on meadows. Although at hatch bill length and body mass did not differ between habitat types, at fledging the bills of chicks hatched on monocultures were *c*. 4% smaller, and any chicks surviving up to that point were *c*. 14–16% lighter than chicks growing up on herb-rich meadows. At fledging, male chicks were lighter and had smaller bills than females, while at hatching both sexes had an equal mass and bill length differed only by 0·4 mm. The sexual size dimorphism thus becomes pronounced during pre-fledging growth. Furthermore, chicks hatched on meadows did not

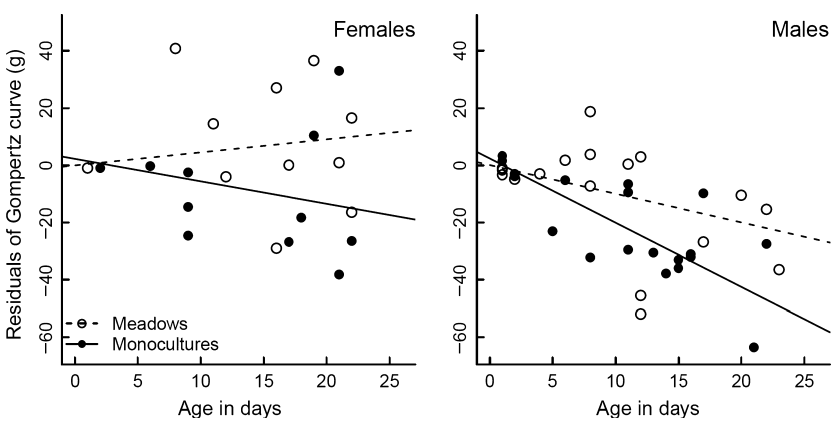

Fig. 3. The relationship between age and residual body mass of recaptured chicks hatched on meadows or monocultures for females and males. Residual body mass is the difference between measured mass and the Gompertz curve predicted mass for chicks of the same age (Beintema & Visser 1989).

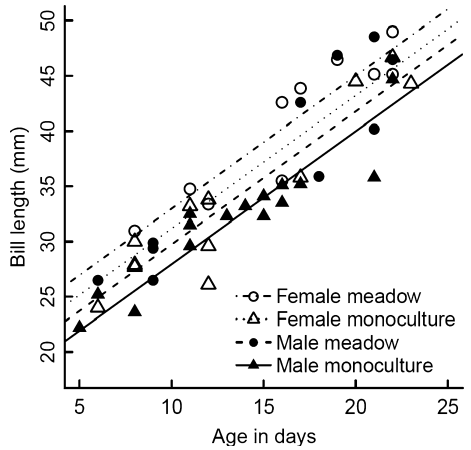

Fig. 4. Bill lengths of female and male recaptured black-tailed godwit chicks hatched in meadows and monocultures.

show difference in growth with chicks hatched in the period 1976–1985 (Beintema & Visser 1989). Note that the differences between habitat types will even be underestimated, as a greater proportion of the chicks on monocultures would have died before recapturing than of the chicks from meadows. That heavier chicks are more likely to survive until fledging than light chicks is consistent with previous studies in Eurasian golden plovers *Pluvialis apricaria* (Pearce-Higgins & Yalden 2002), Eurasian oystercatchers *Haematopus ostralegus* (Kersten & Brenninkmeijer 1995) and western sandpipers *Calidris mauri* (Ruthrauff & McCaffery 2005).

Previous studies have shown differences in food quality between chicks raised on monocultures and herb-rich meadows (Schekkerman & Beintema 2007; Kleijn *et al.* 2010), mainly because intensively managed monocultures were mown during the chick raising period. However, even uncut grassland monocultures will have lower food availability than (uncut) herb-rich meadows, because (i) denser vegetation can make it more difficult to forage (Devereux *et al.* 2004), (ii) the volume of the sward is larger which consequently decreases the density of insects (Kleijn *et al.* 2010) and (iii) the insects on offer are of smaller size (Schekkerman & Beintema 2007; Kleijn *et al.* 2010). The latter becomes a problem when chicks become older; they require larger prey items because energy demands are higher (Schekkerman & Boele 2009). That chicks hatched on monocultures grow more slowly than chicks of meadows agrees with the idea that they have lower energy intake rates.

Slow growth can have long-lasting negative effects well into adulthood (Metcalfe & Monaghan 2001). For Eurasian oystercatchers, van de Pol *et al.* (2006) showed that growing up in low-quality habitat lead to a 2·2 times lower lifetime reproductive success compared with individuals growing up in high-quality habitat. In that case, this was explained by chicks raised in low-quality habitats to have greater chances to end up as breeders in low-quality habitats. In red-billed choughs *Pyrrhocorax pyrrhocorax* fledging under bad environmental conditions lead to reduced reproduction even if conditions improve later in life (Reid *et al.* 2003).

PREDATION RISKS

In the Netherlands, predator densities have increased in the last decades (Schekkerman, Teunissen & Oosterveld 2008), a trend to which agricultural intensification may have contributed (Evans 2004). On cut meadows chicks lose their cover, but on uncut monocultures, the vegetation may be so dense that chicks are obstructed to the extent that they cannot hide successfully (Whittingham & Evans 2004; pers. obs). Moreover, chicks in uncut fields run the risk of being killed during mowing, especially young chicks (Kruk, Noordervliet & ter Keurs 1997; Schekkerman, Teunissen & Oosterveld 2008). Moreover, hungry chicks might show riskier behaviour (Swennen 1989; Brown 1999). Thus, chicks on grassland monocultures are caught between a rock (less food and the need to forage longer) and a hard place (greater detectability by predators while foraging).

MANAGEMENT RECOMMENDATIONS

Agri-environmental schemes (AES) need to provide good-quality habitats to be effective. In the Netherlands, the most popular AES protect nests and chicks from agricultural activities (Musters *et al.* 2001), but do not promote a wet herb-rich grassland habitat with abundant insects (Schekkerman, Teunissen & Oosterveld 2008). More than

Table 5. Model results of the best fit mark-recapture model of chicks marked in the nest (codeflag) and for both models of chicks marked as older chicks with colour ring combinations (models differ with Δ QAICc = 1). Standard errors are given within parentheses

Model	Habitat type	ϕ chick	ϕ adults	p 2nd calendar year	p adult
Code flag					
ϕ(a2-g/.)p(a2)	Meadow	0·13 (0·04)			
	Monoculture	0·04 (0·02)			
	Both		0·62 (0·26)	0·41 (0·13)	0·56 (0·26)
Colour ring combination					
ϕ(a2-./.)p(a2)	Both	0·55 (0·06)	0·96 (0·08)	0·44 (0·06)	0·52 (0·07)
ϕ(a2-g/.)p(a2)	Meadow	0·59 (0·07)			
	Monoculture	0·48 (0·08)			
	Both		0·96 (0·08)	0·44 (0·06)	0·51 (0·07)

two-thirds of the budget (€25 million in 2008) for protecting grassland birds was spent on nest protection and delayed mowing, but 40% of the delayed mowing was carried out before 9 June (van Paasen & Teunissen 2010) when more than half of the chicks from ground-breeding birds have not yet fledged. Today 'meadows' rather than 'monocultures' make up <5% of the Dutch agricultural grassland area in the Netherlands.

Godwit chicks in herb-rich meadows show growth rates similar to those measured in 1976–1985 (Beintema & Visser 1989), while chicks on monocultures show slower growth rates. Schekkerman, Teunissen & Oosterveld (2009) found that chicks growing up on land with 'mosaic management' (an AES where a collective of farmers use staggered mowing to create a mosaic of different grass length, thus providing tall grass throughout the chick phase), also had a lower mass than the chicks from the period 1976–1985. Despite leaving enough 'foraging habitat', these uncut monocultures in general appear to lack the necessary food availability for growing chicks, which is consistent with our claim that chicks need herb-rich vegetation and wet meadows.

Black-tailed godwits hatching nests successfully show greater site-faithfulness than unsuccessful godwits (Groen 1993). In the present case, godwits breeding on monocultures with low-level AES protecting nests only, may be harmed twice: (i) lower chick survival and (ii) birds are constrained from moving to better quality habitat. Such maladaptive habitat choice would speed up the cycle of decline (Gilroy & Sutherland 2007). Our findings imply that AES which focus only on protecting nests from agricultural activities and postponed mowing are not effective in raising chick survival. Even without the possible incumbent problems of maladaptive habitat selection, the growth rate and survival data presented here demonstrate that meadow bird conservation money should be spend on the provision of herb-rich meadows with high groundwater tables that are managed in ways that reflect traditional intensities of land usage. Although reversing grassland monocultures to herb-rich meadows may be difficult to achieve, due to issues such as residual nitrogen levels in soils (Bakker & Berendse 1999), it can increase diversity of insects and flora (Vickery *et al*. 2001), and numbers of grassland breeding birds such as northern lapwing *Vanellus vanellus* (Eglington *et al*. 2010) and redshank *Tringa totanus* (Smart *et al*. 2006).

Is investing in more herb-rich meadows sufficient to halt the population decline of godwits, if chick survival would increase to 0·14? Adults have annual survival rates between 0·8 and 0·9 (Roodbergen, van der Werf & Hötker 2012), and hatch 3·7 eggs per successful nest (R. Kentie *et al*., unpubl. data). Assuming that godwits (i) first breed in their 3rd calendar year (Groen 1993), (ii) do not disperse to monocultures and (iii) after a failed attempt, there is a possibility of 0·5 to lay another clutch, the population would be stable if 32% of the nests hatch if the adult survival rate is 0·9. If adult survival rate is 0·8, then 93% of the nests should hatch for a population to remain stable. In our study area, from 2007 to 2010, of the nests on herb-rich meadows 54% hatched (R. Kentie *et al*., unpubl. data). On this basis, a population would be stable at an adult survival of 0·85. Although more fine-tuned demographic analyses are needed, this exercise makes clear that, without management adjustments to improve habitat quality, black-tailed godwits on grassland monocultures are doomed.

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